

TWO NEW NEOTROPICAL TREEHOPPER GENERA AND INVESTIGATION OF  
THE PHYLOGENY OF THE SUBFAMILY MEMBRACINAE  
(HOMOPTERA: MEMBRACIDAE)

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*Abstract.*—Two new genera are described in the membracid tribe Membracini: *Havilandia*, new genus, including *H. pruinosa* (Haviland), new combination, and *H. hypso-proroides*, new species; and *Lewdeitzia*, new genus, including *L. lunata*, new species. *Havilandia* is morphologically and behaviorally similar to Talipedini and some *Leioscyta* Fowler (Membracini), but may be the sister-group of Hypso prorini. *Lewdeitzia* is apparently dimorphic for a feature of the forewing venation used to distinguish *Erechtia* Walker from *Leioscyta*. Preliminary cladistic analyses of 27 taxa in the subfamily Membracinae place the new genera among others in the tribe Membracini, but suggest that this tribe is paraphyletic, having given rise to other tribes in the subfamily. The analyses further suggest that the tribe Talipedini is paraphyletic and the genera *Leioscyta* and *Membracis* Fabricius are para- or polyphyletic. Reclassification of the Membracinae is needed, but should await elucidation of the limits of some genera of Membracini by more extensive cladistic analyses. A key to the tribes of Membracinae and the genera of Membracini is presented. Nomenclatural changes include restoration of the original spelling of *Paragara* Goding, 1926, and of the combination *P. tholoidea* (from *Paragargara*) and two new combinations, *Paragara nigra* (Funkhouser) (from *Paragargara*) and *Enchenopa beebei* (Haviland) (from *Leioscyta*). Two species most recently treated as *Membracis* are here considered Membracini *incertae sedis*.

*Key Words:* Cladistics, evolution, morphology, parsimony, paraphyly

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The subfamily Membracinae constitutes a major component of treehopper diversity in the New World and is especially diverse in the tropics. The North American *Enchenopa binotata* species complex, whose females insert eggs into host plant tissue, has attracted attention as an example of host-mediated sympatric speciation (Wood 1993b). Polyphagy has been reported within

some tropical genera (Loye 1992, Wood 1993a) and may be explained partly by the habit in many species, but in Membracinae only, of depositing egg masses on the host plant surface, thereby obviating many of the plant's first-line structural and chemical defenses against herbivore colonization.

Cladistic analyses of the family-group taxa of Membracidae (Dietrich and Deitz 1993; Dietrich, Deitz, and McKamey, unpubl.) support the monophyly of Membracinae, but, until now, there has been no explicit cladistic analysis of relationships among its

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five tribes (Deitz and Dietrich 1993): Aconophorini, Hoplophorionini, Hypsoprorini, Talipedini, and Membracini. Nonetheless, three are supported by apparent synapomorphies. The Aconophorini and Hoplophorionini are well-supported monophyletic groups (Dietrich and Deitz 1991; McKamey and Deitz, unpubl.). The species of Hypsoprorini are also united by apparent synapomorphies that are unique among the Membracinae: pronotum with lateral margins of posterior process overlapping forewing at rest, and clavus of forewing acute and extensively associated with apical limbus. No synapomorphies have been found to support the monophyly of Talipedini or Membracini.

The tribe Talipedini was erected (Deitz 1975) to draw attention to the position of *Trinarea* (as *Talipes*) *appendiculata* (Fonseca) as morphologically intermediate between the tribes Membracini and Hoplophorionini. Talipedini and Hoplophorionini both have clavate hind tibiae and small hind tarsi, a unique synapomorphy, but features used by Deitz (1975) to distinguish Talipedini from Hoplophorionini are present in Membracini, suggesting that Talipedini may be paraphyletic. McKamey and Deitz (1991) transferred two more species into Talipedini, but did not list additional diagnostic features for the tribe.

The most diverse tribe in the subfamily is Membracini, which, now with 17 genera and nearly 200 described species, is twice as rich in genera and species as the next largest tribe, Hoplophorionini. Among the diagnostic features listed by Deitz (1975) for Membracini, none are unique to that tribe. Thus, Membracini (*sensu* Deitz 1975, expanded by McKamey 1992 and Sakakibara 1992), although defined by a unique combination of features, also may be paraphyletic.

Two new taxa were discovered that keyed to Membracini (Deitz 1975), but were not assignable to any known genus and have combinations of features traversing current

concepts of tribes and genera. Species of *Havilandia*, new genus, share morphological features with species of Hypsoprorini, Hoplophorionini, Talipedini, and Aconophorini. *Lewdeitzia lunata*, new genus, new species, may be sexually dimorphic for the forewing venation feature distinguishing *Leioscyta* Fowler from *Erechtia* Walker (tribe Membracini) and the female has a broad, obtusely rounded, marginally compressed, anterior pronotal horn similar to that of Aconophorini and some Hoplophorionini. The features of these new taxa accentuate problems with the generic and tribal classification of the Membracinae. To help place the new taxa, we analyzed the relationships among the genera of Membracini and representatives of other tribes of Membracinae.

Given the need of further taxonomic work revealed by the cladistic analysis, the numerous modifications to Membracini since the last key (Funkhouser 1951), and the discovery of some previously unknown or neglected intrageneric variation, we present a key to tribes of Membracinae and genera of Membracini to clarify current taxonomic concepts in the subfamily.

#### KEY TO THE MEMBRACINAE

1. Forewing vein R initially divided into  $R_{1+2+3}$  and  $R_{4+5}$  or venation reticulate, or with both conditions ..... 2
- 1'. Forewing vein R initially divided into R, and  $R_s (=R_{2+3+4+5})$  (Figs. 1, 2), venation not reticulate ..... 4
2. Metathoracic legs with tibiae clavate and with tarsi distinctly shorter than anterior tarsi ..... Hoplophorionini<sup>1</sup>
- 2'. Metathoracic legs with tibiae not clavate and with tarsi as long as anterior tarsi (Fig. 2c) ... 3
3. Pronotum with lateral margins of posterior process overlapping portions of apical limbus and veins of forewing in repose; forewing clavus acuminate ..... Hypsoprorini<sup>2</sup>

<sup>1</sup> Key to genera in prep. by McKamey and Deitz.

<sup>2</sup> See Funkhouser's (1951) key to genera of "Notocerini," plus *Jibarita* Ramos and *Hypsoprachis* Fonseca and Diringshofen.

- 3'. Pronotum evenly tapered posterolaterally, at most concealing part of apical limb of forewing in repose; forewing clavus oblique apically ..... Aconophorini<sup>3</sup>
- 4. Metathoracic legs with tibiae clavate and with tarsi distinctly shorter than anterior tarsi; abdomen with middorsal tuberosities ..... Talipedini (monotypic: *Trinarea* Goding)
- 4'. Metathoracic legs with tibiae not clavate (Fig. 2c) or, if clavate, then abdomen without middorsal tuberosities; metathoracic tarsi at least as long as anterior tarsi (Membracini) ..... 5
- 5. Metathoracic tibiae clavate, with dorsal edges flattened, and with cucullate setae numerous and small in row I, small or absent in row II (Fig. 1j) ..... *Havilandia*, n. gen.
- 5'. Metathoracic tibiae with dorsal edges not flattened, with large cucullate setae in rows I and II (Fig. 2c) ..... 6
- 6. Pronotal metopidium with 1 to several oblique carinae on each side and with pair of dorsolateral carinae or dorsum strongly bisinuate posteriorly, or with all three conditions ..... 7
- 6'. Pronotal metopidium without oblique carinae, with or without dorsolateral carinae, dorsum sublinear or once-sinuate posteriorly ..... 13
- 7. Pronotal lateral carinae extending to posterolateral margins or nearly so; pronotal integument coarsely punctate (pits distinct) and thick ..... 8
- 7'. Pronotal lateral carinae terminating before or above humeral angles; pronotal integument sometimes smooth (pits indistinct), membrane-like ..... 9
- 8. Pronotum bisinuate, declining stepwise from above humeral angle to posterior apex ..... *Tylopetta* Fowler
- 8'. Pronotum declining evenly from above humeral angle to posterior apex ..... *Campylenchia* Stål, *Enchenopa* Amy. & Serv.
- 9. Pronotum and its horn depressed, pronotal integument thick and coarsely punctate (pits large, deep, and distinct above humeri) ..... *Kronides* Kirkaldy
- 9'. Pronotum and its horn, if present, foliaceous, thin, and smooth (pits small, shallow, and indistinct above humeri at least) ..... 10
- 10. Pronotal horn present and distinct ..... *Enchophyllum* Amy. & Serv.
- 10'. Pronotal horn absent or indistinct ..... 11
- 11. Pronotal metopidium with a pair of dorso-lateral carinae and a ventral lobe produced in front of the vertex of the head ..... *Phyllotropis* Stål
- 11'. Pronotal metopidium without dorsolateral carinae or without ventral lobe, or with neither feature ..... 12
- 12. Pronotal dorsum strongly foliaceous, sides extensively compressed into a single plate-like median carina ..... *Folicarina* Sakakibara<sup>4</sup>
- 12'. Pronotal dorsum not so strongly compressed, sides not extensively fused ..... *Membracis* (in part; e.g. *M. carinulata* Richter)
- 13. Pronotum foliaceous and smooth (pits small, shallow, and indistinct above humeri at least); forewing surface coriaceous throughout (arcuate chaetoids conspicuous) ..... *Membracis* (in part; e.g. *M. foliata* [L.])
- 13'. Pronotum depressed, at least posterolaterally, and more coarsely punctate (pits larger, deeper, and distinct above humeri); distal forewing surface more glossy (arcuate chaetoids absent or inconspicuous) ..... 14
- 14. Anteromedial pronotal horn present (except in some ♂ *Tritropidia*, which are indistinguishable from *Leioscyta*) ..... 15
- 14'. Anteromedial pronotal horn absent ..... 16
- 15. Pronotal horn narrow in lateral aspect; clypeus distally narrowed (as in Fig. 1h) ..... *Tritropidia* Stål
- 15'. Pronotal horn broad in lateral aspect; clypeus distally truncate (Fig. 2g) ... *Lewdeitzia*, n. gen.
- 16. Forewing with 2 or more r-m crossveins ... 17
- 16'. Forewing with only 1 r-m crossvein ..... 18
- 17. Pronotum rugosely carinate, steeply declivous posteriorly, humeri without transverse carinae ..... *Bolbonotodes* Fowler
- 17'. Pronotum evenly carinate, gradually declivous posteriorly, humeri often with transverse carinae ..... *Erechtia*
- 18. Pronotal dorsum with irregular gibbositities throughout, transversely carinate or gibbous subapically, and without long straight lateral carinae; mesothoracic tibiae foliaceous ..... *Bolbonota* Amy. & Serv.
- 18'. Pronotal dorsum without irregular gibbositities, usually with 1 pair sublinear lateral carinae extending posteriorly over dorsum; mesothoracic tibiae cylindrical to foliaceous ... 19
- 19. Pronotal contour in lateral aspect strongly sinuate ..... *Paragara*<sup>5</sup>

<sup>3</sup> See Dietrich and Deitz (1991) for keys to genera and species.

<sup>4</sup> New distribution record for *Folicarina* nr. *bicolor*: Trinidad, Arima Valley, St. Andrew's Trace, 16–24 June 1981, leg. S.H. McKamey.

<sup>5</sup> *Paragara* Goding, 1926a; original spelling here restored from *Paragargara*. Type species: *Paragara tho-*

- 19'. Pronotal contour in lateral aspect linear or nearly so ..... 20  
 20. Hind wing without r-m and m-cu crossveins, with vein M free ..... *Eunusa* Fonseca  
 20'. Hind wing with 1 r-m and 1 m-cu crossvein ..... *Leioscyta*

#### DESCRIPTIONS OF NEW TAXA

Morphological terms, techniques, and the convention for quoting labels follow Deitz (1975), Dietrich (1989), and Dietrich and Deitz (1991), except forewing crossvein *s* (that connects veins  $R_{2+3}$  and  $R_{4+5}$ ) equals "r" of Deitz (1975). Specimens for this study were provided by The Natural History Museum, London (BMNH); North Carolina State University, Raleigh (NCSU); the personal collection of S. H. McKamey (SHMC); and the United States National Museum of Natural History, Washington (USNM). Character states for taxa other than those described below are based on material identified and labeled in the NCSU and USNM collections.

#### Tribe Membracini Rafinesque

#### *Havilandia*, NEW GENUS

(Figs. 1a-k)

*Type species: Tropidoscyta pruinosa* Haviland.

**Diagnosis.**—Metathoracic tibia clavate and compressed along dorsal edge, with setal row I bearing numerous small cucullate setae and row II with few or none; forewing with cell membranes clothed by erect macrotrichia, without crossvein *s*.

**Description.**—*Head:* Vertex (Fig. 1h) impressed mesad of ocelli, ventrolateral margins weakly produced; ocelli approximately 2× as far from each other as from mesal margins of eyes and approximately 1 ocellar diameter from dorsal margin of ver-

tex; frontoclypeus flat, diamond shaped, margins weakly produced, cibarial muscle scars parallel to ventrolateral margins; frontoclypeus, clypellus, and rostrum, in lateral view (Figs. 1a, i) forming continuous arc, rostrum extended to base of abdomen; in anterior view with distance between lateral margins of eyes slightly less than distance between pronotal humeri. *Thorax:* Pronotum (Figs. 1a, h-i) elongate and with midline strongly carinate and with 1 dorsolateral pair of strong carinae diverging from apex, extending to posterolateral margin of pronotum. Forewing (Figs. 1a, i) punctate in basal half between veins C and M and in anal area, vein R initially divided into  $R_1$  and  $R_s$ , crossveins *s* and r- $m_1$  absent, 2 m-cu crossveins present, apical limb relatively narrow, contiguous with clavus for short distance only. Hind wing with crossveins r-m and m-cu present. *Legs:* Pro- and mesothoracic tibiae (Fig. 1i) compressed, translucent, margins of prothoracic tibia not expanded, mesothoracic tibia with posterior margin slightly expanded; mesothoracic coxa without acute process; metathoracic femur with pair of dorsoapical cucullate setae; metathoracic tibia (Figs. 1b, j) clavate, posterior margin compressed, row I with 15 or more small cucullate setae, row II with 5 or fewer, row III absent; all tarsi subequal in length; metathoracic tarsus relatively slender, tarsomere I with small apical cucullate seta. *Abdomen:* Sternum III without median tubercle, transverse carina indistinct or absent; terga without tuberosities or fenestrae. *Male:* Pygofer (Fig. 1d) with weak vertical lateral carina; lateral plate free, unarmed; aedeagus (Figs. 1f-g) with shaft slender, tapering apically, anterior face of apex evenly denticulate; gonopore membrane, in posterior view, occupying apical half of shaft; shank of style (Fig. 1e) slightly expanded preapically, shank sparsely setose, apex recurved, acute, in posterior view oriented dorsolaterally; subgenital plate with preapical dorsal lobe. *Female:* Posterior margin of sternum VII with arcuate emargination;

*loidea* Goding, 1926a, by original designation. Restored combination: *Paragara tholoidea* Goding. New combination: *Paragara nigra* (Funkhouser 1940). *Paragargara* (Goding 1926b) was an incorrect subsequent spelling and has no availability. *Paragargara* Goding, 1929, was an unjustified emendation and is an objective junior synonym of *Paragara*.

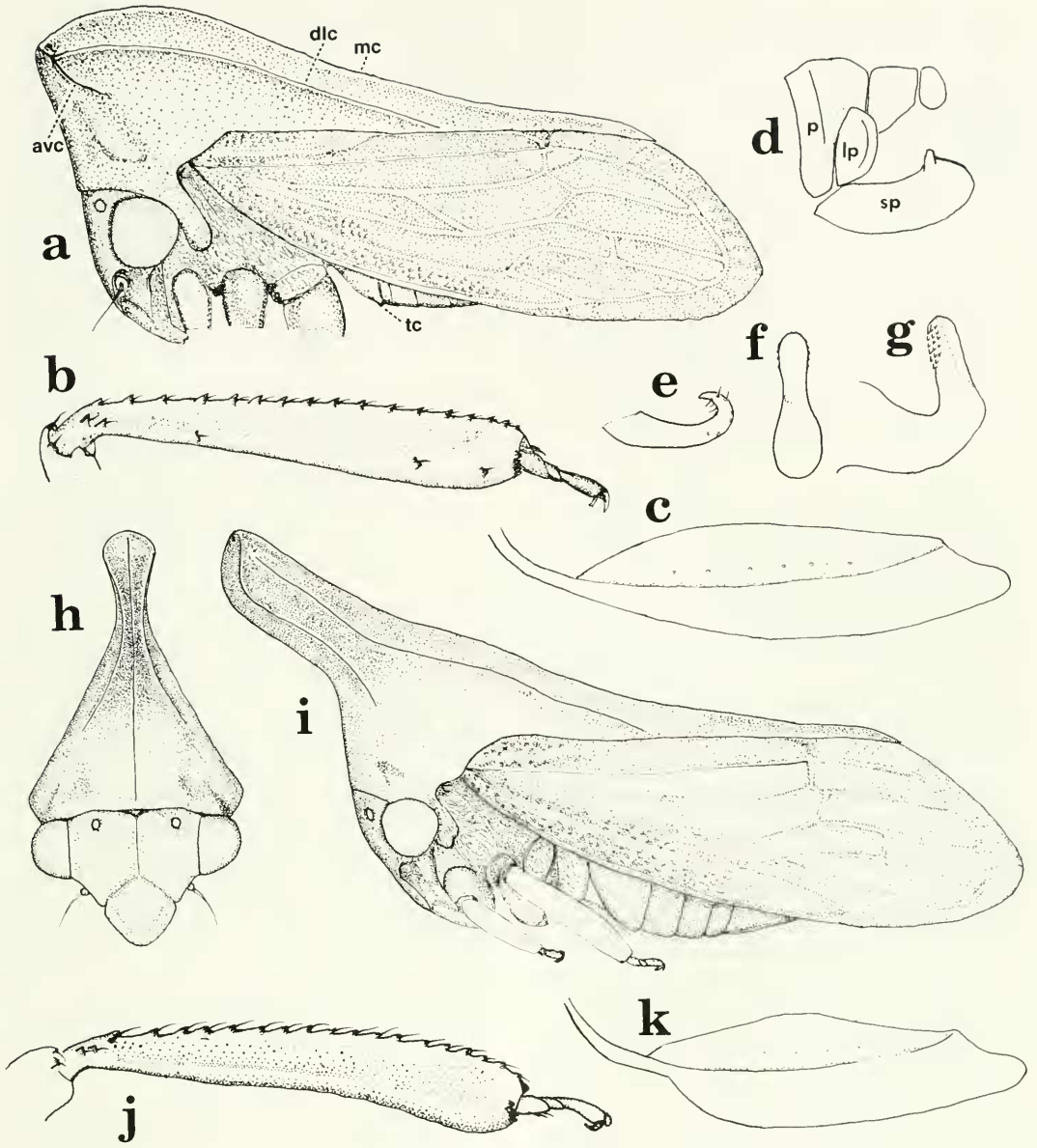


Fig. 1. *Haviglandia*, new genus. a-g, *H. pruinosa* (Haviland). a-c, holotype ♀: a, habitus, lateral view; b, left metathoracic tibia and tarsus, lateral view; c, second valvulae, lateral aspect; d-g, #7-90-337g ♂: d, terminalia, lateral view (genitalia removed); e, shank of left style, ventrolateral view; f-g, aedeagus, posterior and lateral views, respectively. h-k, *H. hypsoproridae*, new species, holotype ♀: h, head and pronotum, anterior view; i, habitus, lateral view; j, left metathoracic tibia and tarsus, lateral view; k, second valvulae, lateral view. avc, anteroventral carina; dlc, dorsolateral carina; dsc, dorsal submedial carina; p, pygofer; mc, median carina; lp, lateral plate; sp, subgenital plate; tc, transverse sternal carina.

2nd valvulae (Figs. 1c, k) in lateral view gradually expanded toward midlength, then tapering slightly toward apex, dorsal margin with arcuate emargination preapically, without distinct crenulae or teeth. *Integumental vestiture*: Vertex and pronotum evenly punctate; forewing membrane with semi-erect pale setae. Abdominal terga coarsely punctate, most pits associated with lateral seta; acanthae simple to dentate.

Notes and etymology.—Short-horned specimens of this genus resemble *Leioscyta* Fowler, but are distinguishable by the presence of a pair of anteroventral longitudinal carinae on the pronotum and the non-foliateous front tibiae. Long-horned specimens resemble *Hypsoprora* Stål (Hypsoprorini), but lack apicolateral expansions on the posterior pronotal process. Although *Havilandia* best fits Deitz's (1975) concept of the tribe Membracini, certain features of the new genus resemble those of other tribes. Like species of Hoplophorionini and Talipedini, *Havilandia* has clavate hind tibiae with a reduced number of cuculate setae in row II. Like some species of Hypsoprorini, the new genus has a ventrolateral pair of carinae on the pronotal horn.

Generic recognition is based primarily on the tibial and abdominal features, but both species also have: vertex densely clothed with pale setae; thoracic pleuron pilose, setae clothed with white waxlike material; pronotum produced anterodorsally, with 1 ventrolateral pair of strong carinae diverging from the apex; and forewings densely clothed with arcuate chaetoids.

This genus is named in honor of Maud D. Haviland, a pioneer in the ecology and taxonomy of Neotropical Membracidae.

***Havilandia pruinosa* (Haviland),**

NEW COMBINATION

(Figs. 1a–g)

*Synonymy*: *Tropidoscyta pruinosa* Haviland, 1925:237.

*Type locality*: Kartabo, Cuyuni District, Guyana [BMNH].

Material examined.—Holotype ♀ [BMNH]. Other specimens: Nestor, Trinidad; San Martin and Shapajilla, Peru; and Culebra, Amazonas, Venezuela [all USNM]; road to Foco Mine, 33 km SE El Dorado, Bolivar, Venezuela [SHMC]. Dates of collection: February, April, May, August. A teneral ♂ specimen from Maroni, French Guiana [Figs. 1d–g; Dietrich Research #7-90-337g, NCSU] is probably conspecific with the holotype of *H. pruinosa* but lacks a pale macula on the forewing at the apex of vein Cu that is present in the holotype (Fig. 1a).

Notes.—Females of *H. pruinosa* guard their eggs and are not ant-attended (Haviland 1925), characteristics shared with Hoplophorionini and some Aconophorini and Membracini (Haviland 1925, Wood 1984, Dietrich and Deitz 1991). *H. pruinosa* females also deposit a pale waxlike material in spirals along the twig and leaf edges in the vicinity of their egg masses (Haviland 1925; McKamey, unpubl.). Similar deposits are produced by *Leioscyta spiralis* Haviland (Haviland 1925, Strümpel 1986) (tribe Membracini), an additional (unidentified) *Leioscyta* species (McKamey, unpubl.), *Ochropepla triangulum* (Germar) (tribe Hoplophorionini; Wood 1984 [as *O. pallens* Stål]), and *Aconophora mexicana* Stål (tribe Aconophorini; Wood 1984, Dietrich and Deitz 1991). Nymphs of *H. pruinosa*, *L. spiralis*, and *A. mexicana* are also clothed with irregular waxlike exudates that facilitate crypsis among the spiral deposits (as in Strümpel 1986: Fig. 2). Many other species of Membracinae have nymphs with white waxlike exudates but lack waxy deposits adjacent to their egg masses. Such features have not been reported for species of subfamilies other than Membracinae.

***Havilandia hypsoprroides*,**

NEW SPECIES

(Figs. 1h–k)

*Type locality*: Fonteboa, Amazonas, Brazil [BMNH].

Description.—Head, pronotum, and ab-

domen reddish brown, pronotal horn darker than rest of pronotum, legs yellow; head with vertex densely clothed with pale setae; thoracic pleuron pilose, setae clothed with white waxlike material; forewing membrane uniformly smoky hyaline. Pronotum (Fig. 1i) produced into an elongate, slender antero-medial horn, apex in lateral view expanded and obliquely rounded, with 1 ventrolateral pair of strong carinae diverging from apex; posterior process approximately even with crossvein r-m of forewing at rest, apex slightly elevated. Forewing densely clothed with arcuate chaetoids. Metathoracic tibia (Fig. 1j) with setal row I bearing 15–18 cucullate setae. *Dimensions* (mm): Body length (head to apex of forewing at rest) 5.1, width across humeri 1.7; vertex height 0.7, width 1.0; pronotum length 5.3; head to horn apex 2.1; forewing length 4.5; prothoracic tibia length 1.0; metathoracic tibia length 1.5; ovipositor length 1.0.

Material examined.—Holotype ♀ labeled: “Amazon./ Fonteboa; Riksmuseum/ Stockholm; Dietrich Res./ 7-90-33a2; HOLOTYPE/ Havilandia/ hypsoprroides/ Dietrich and McKamey” [BMNH].

Etymology.—The trivial name was selected to indicate the similarity of this species to members of the genus *Hypsoprora* Stål.

#### KEY TO SPECIES OF *HAVILANDIA*

1. Anterior pronotal process, in lateral view, short, broad, and tapered, apex rounded (Fig. 1a) . . .  
     . . . . . *pruinosa* (Haviland)
- 1'. Anterior pronotal process, in lateral view, elongate and slender, apex obliquely truncate (Fig. 1i) . . . . . *hypsoprroides*, n. sp.

#### *Lewdeitzia*, NEW GENUS

(Figs. 2a–m)

*Type species:* *Lewdeitzia lunata*, new species.

*Diagnosis.*—Anterior region of pronotum in lateral view elevated into broad, rounded process with 1 carina on each side, in female further developed into large, marginally

compressed horn; forewing with 1 or 2 r-m crossveins, with vein R initially divided into R<sub>1</sub> and R<sub>s</sub>.

*Description.*—*Head:* Vertex (Fig. 2g) not impressed mesad of ocelli, ventrolateral margins foliaceous and strongly produced; ocelli approximately 2× as far from each other as from mesal margins of eyes and approximately 2 ocellar diameters from dorsal margin of vertex; frontoclypeus flat, lateral corners rounded and apex truncate, margins foliaceous; rostrum extended to base of abdomen; frontoclypeus, in lateral view, forming shelf above clypellus; in anterior view (Fig. 2g) with distance between lateral margins of eyes slightly less than distance between humeri. *Thorax:* Pronotum with broad, marginally compressed anterodorsal process, much larger in female (Fig. 2a) than in male (Fig. 2e), bearing pair of lateral carinae extending ventrolaterally from apex but not attaining posterolateral margins. Forewing (Figs. 2a, e) punctate in basal half between veins C and M and in base of anal area, vein R initially divided into R<sub>1</sub> and R<sub>s</sub>, crossveins s and r-m<sub>2</sub> present, with crossvein r-m<sub>1</sub> present (Fig. 2a) or absent (Fig. 2e), 2 m-cu crossveins present, m-cu, perpendicular to veins M and Cu, 1st and 2nd M cells subequal in length, apical limb relatively wide, contiguous with clavus for short distance only. Hind wing crossveins r-m and m-cu present. *Legs:* Pro- and mesothoracic tibiae (Figs. 2h, i) compressed and foliaceous; mesothoracic femur with anteroapical cucullate seta; metathoracic tibia (Fig. 2c) straight, not compressed, row I with 7–8 enlarged cucullate setae, row II with 4–5 enlarged cucullate setae, row III without cucullate setae; metathoracic tarsus slightly longer than others, tarsomere I with 4 apical cucullate setae. *Abdomen:* Sternum III without median tubercle, sternum IV with distinct transverse carina; terga without tuberosities or fenestrae. *Male:* Pygofer with vertical lateral carinae; lateral plate free, with prominent rounded vertical ridge over entire height (Fig. 2j); aedeagus

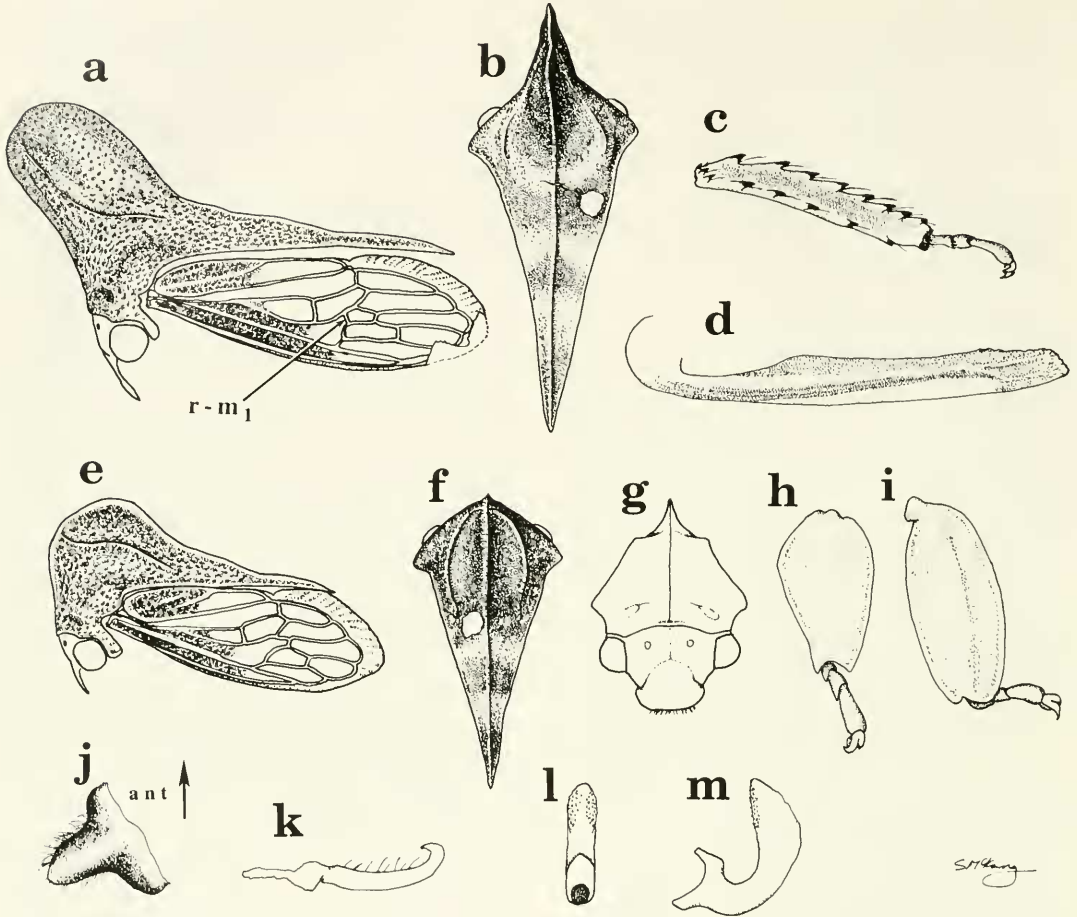


Fig. 2. *Lewdeitzia lunata*, new genus, new species. a-d, holotype ♀: a, head, pronotum, and forewing, lateral view (texture); b, head and pronotum, dorsal view (color); c, reversed right metathoracic tibia and tarsus, lateral view, same scale as 2h-i; d, second valvulae, lateral view; e-m, ♂: e, head, pronotum, and forewing, reversed lateral view (texture); f-g, head and pronotum, dorsal (color) and anterior views, respectively; h-i, left pro- and mesothoracic tibiae and tarsi, lateral views; j, left lateral plate, dorsal view (ant, anterior); k, left style, ventrolateral view; l-m, aedeagus, anterior and lateral views, respectively.

(Figs. 2l, m) with shaft slender, in anterior view subparallel, in lateral view tapering apically, anterior face of apex evenly denticulate laterally; gonopore membrane, in posterior view, occupying nearly entire width of shaft; shank of style (Fig. 2k) with numerous long setae, apex recurved and acute; subgenital plate evenly tapering apically, without lobes. *Female*: Posterior margin of sternum VII with arcuate emargination; 2nd valvulae, in lateral view (Fig. 2d), subparallel, apical  $\frac{1}{3}$  irregularly cren-

ulate. *Integumental vestiture*: Vertex and pronotum coarsely punctate, sparsely clothed with pale recumbent setae; thoracic pleuron sparsely setose, setae not clothed with waxlike material; forewing membrane glabrous. Abdominal terga coarsely punctate, pits without lateral setae; acanthae dentate.

*Notes and etymology*.—The female of this genus resembles *Aconophora* Fairmaire (Aconophorini), while the male resembles *Leioscyta*. The genus is named to honor



Lewis L. Deitz, whose higher classification and bibliographies have greatly facilitated research on the Membracoidea.

***Lewdeitzia lunata*, NEW SPECIES**

(Figs. 2a–m)

*Type locality*: São Paulo, São Paulo State, Brazil [NCSU].

*Description*.—Ground color brown; pronotal carinae, crescent-shaped band around posterior base of horn (female; Fig. 2b) or mottling between carinae and humeri (male; Fig. 2f), 2 transverse bands farther posterad on dorsum, transverse band on metopidium between humeri, and legs paler orange brown; forewing smoky hyaline with 2 pale transverse bands (1 near base, 1 aligned with end of clavus). Female pronotal horn with apically bifid lateral longitudinal gibbosity, apex obtusely rounded, lateral carinae weak, terminating slightly posterad of humeri; male horn short and rounded, carinae distinct, marginal compressed area narrower. Other morphology as described for genus.

*Dimensions (mm)*.—Body length ♀ 6.3, ♂ 5.3; maximum width ♀ 2.8, ♂ 2.4; pronotal length ♀ 7.0, ♂ 4.5; head to horn apex ♀ 3.3; forewing length ♀ 5.5, ♂ 4.8; prothoracic tibia length ♀ 1.5, ♂ 1.2; metathoracic tibia length ♀ 2.2, ♂ 1.9; ovipositor length 1.9.

*Material examined*.—Holotype ♀ labeled: "Sao Paulo/ S. Paulo Brazil/ Nov. 1930; A.Maller,Coll./ FrankJohnson/ Donor; 1531 ♀/ S. Paulo/ S. Paulo/ 10.30; HOLOTYPE/ Lewdeitzia/ lunata/ Dietrich and McKamey" [NCSU]. Other material: ♂ from Corupá, Santa Catarina, Brazil, XI-1929, A. Maller, Coll. (Dietrich Research 15-91-40 ♂) [NCSU].

*Notes and etymology*.—The holotype lacks its left metathoracic leg. The male, which lacks its left hind tarsus and right hind tarsomeres II and III, was excluded from type status because it may not be conspecific, given the considerable differences compared to the female. Nonetheless, because extreme sexual dimorphism is com-

mon in other species of Membracinae (e.g. see Sakakibara 1976 and Strümpel and Strümpel 1978), we consider the nearly identical color pattern and similar size of both *Lewdeitzia* specimens sufficient to regard them as a single species. The species name is derived from Latin for the pale crescent-shaped band around the base of the female's horn.

CLADISTICS

Morphological characters

Head

1. Frontoclypeus: 0, apex in lateral view not forming a shelf over clypellus, margins not expanded laterally (Fig. 1h); 1, apex in lateral view not forming a shelf over clypellus, margins expanded laterally; 2, apex in lateral view forming a shelf over clypellus (Sakakibara 1992: Figs. 1, 2, 4).

Pronotum

2. Shape: 0, depressed or rounded (Figs. 1a, i); 1, compressed (Deitz 1975: Fig. 15S); 2, foliaceous (*op. cit.*: Fig. 15U).

3. Anteromedial horn: 0, absent or weak (Fig. 1a); 1, well developed (Fig. 1i). Although entirely enclosed by the foliaceous pronotal margins, the horns of *Phyllotropis* and *Folicarina* are nonetheless well indicated (Sakakibara 1992: Figs. 3, 4).

4. Transverse metopidial carinae: 0, absent; 1, restricted to humeri; 2, complete, two sides meeting medially.

5. Dorsolateral carinae: 0, absent; 1, one submedial pair (Figs. 1a, i); 2, two or more pairs (Deitz 1975: Fig. 15R). The pronotal carinae of Hoplophorionini converge at the base of the metopidium rather than at its apex, as in other Membracinae, and therefore may not be homologous.

6. Posterior extension of dorsolateral carinae: 0, absent; 1, terminated above humeri; 2, extended beyond humeri.

7. Dorsal submedial carinae: 0, absent; 1, meeting medial carina anteriorly (Fig. 1a); 2, not meeting medial carina anteriorly.

8. Anteroventral pair of carinae, which are contiguous with dorsolateral carinae: 0, absent; 1, present (Figs. 1a, h, i).

9. Irregular, oblique metopidial carinae: 0, absent; 1, present (Sakakibara 1992: Fig. 4).

10. Posterior transverse carina: 0, absent; 1, present (Haviland 1925: Pl. II, Fig. 6).

11. Posterior sublateral longitudinal carinae: 0, absent; 1, present (Fonseca and Diringshofen 1969: Fig. 3). Our treatment of this feature as a separate character from character 6 is supported by the presence of both dorsolateral and sublateral carinae in some taxa (e.g. *Erechtia*).

12. Punctuation: 0, coarse—distance between pits less than pit diameter, pits distinct above humeri; 1, fine—distance between pits greater than pit diameter, pits indistinct above humeri. Considerable variation exists among taxa coded as state 0, but state 1 (e.g. *Membracis*) is distinctive (compare Figs. 7 and 10 of Wood and Morris 1974).

#### Pleuron and legs

13. Pleural wax: 0, absent; 1, present. State 1 is considered to represent a homology, although *Havilandia* has the pleuron densely pilose with waxy setae while *Hypsoprora* has the pleuron sparsely setose with waxlike deposits on the surface of the sclerite.

14. Pro- and mesothoracic tibiae: 0, narrow, semicylindrical; 1, subfoliaceous (Figs. 2h, i).

15. Mesothoracic acute coxal process: 0, absent; 1, present. State 1 is a synapomorphy of the tribe Hoplophorionini.

16. Metathoracic tibia: 0, not clavate, row II with numerous cucullate setae (Fig. 2a); 1, distinctly clavate, row II with few or no cucullate setae (Figs. 1b, j). Some *Erechtia* and *Leioscyta* species have the metathoracic tibia weakly clavate, but with numerous cucullate setae in row II, perhaps representing an intermediate state of this character.

17. Length of metathoracic tarsi relative to pro- and mesothoracic tarsi: 0, longer; 1, subequal; 2, distinctly shorter (Deitz 1975: Fig. 14A).

#### Forewing

18. Vein R: 0, initially divided into R<sub>1</sub> and R<sub>s</sub> (Fig. 1a); 1, initially divided into R<sub>1+2+3</sub> and R<sub>4+5</sub> (Deitz 1975: Fig. 11A).

19. Crossvein s: 0, absent; 1, present (Figs. 2a, e).

20. Crossvein(s) r-m: 0, one (Figs. 1a, i); 1, two or more (Fig. 2a).

21. Membrane, erect macrotrichia: 0, absent; 1, present.

22. Membrane, arcuate chaetoids: 0, absent, surface glabrous; 1, present, surface shagreen (Dietrich and Deitz 1993: Fig. 27).

#### Abdomen

23. Sternum III: 0, unarmed; 1, with medial tubercle; 2, with transverse carina (Fig. 1a).

24. Sternum IV: 0, unarmed; 1, with transverse carina (Deitz 1975: Fig. 3A).

25. Dorsal tuberosities or fenestrae, terga V–VIII: 0, absent; 1, paired (*op. cit.*: Fig. 3A); 2, unpaired medial (Dietrich 1989: Fig. 18). The presence, in *Trinarea* and some *Erechtia*, of paired tuberosities on the anterior terga and unpaired medial tuberosities on the posterior terga suggests that one feature was derived from fusion or separation of the other.

#### Second valvulae

26. Length: 0, elongate; 1, short and broad (Deitz 1975: Figs. 17H–J).

27. Dorsal teeth (*op. cit.*: Figs. 17C, M): 0, absent; 1, one; 2, two. The serrations found in many membracid groups (*op. cit.*: Fig. 8) were not considered homologous.

28. Dorsoapical emargination: 0, absent; 1, present (Figs. 1c, k).

#### Analysis

Our data matrix (Table 1) included at least one representative of each genus of Mem-

Table 1. Character state matrix for numerical cladistic analysis of the Membracinae. Missing values are represented by ?'s.

OTU	Character				
	1-5	6-10	11-15	16-20	21-28
<b>Heteronotinae (outgroup)</b>					
<i>Dysyncritus intectus</i> Fowler	20000	00000	00000	00010	00000000
<b>Membracinae</b>					
Aconophorini ( <i>Guayaquila</i> Goding)	00100	00000	00010	01110	01011000
Hypsoprorini ( <i>Hypsoprora</i> Stål)	20101	11100	00110	00110	01010020
Hoplophorionini ( <i>Potnia</i> Stål)	00102	22000	10001	12110	00012000
<b>Membracina</b>					
<i>Bolbonota</i> sp.	10002	22001	00010	01010	01010100
<i>Enchenopa binotata</i> (Say)	21101	21010	00010	00010	01011020
<i>Enchophyllum</i> sp. A	21101	11010	01010	00010	01011020
<i>Enchophyllum</i> sp. B	21101	11000	01010	00010	01011020
<i>Erechtia bicolor</i> Walker	20022	21000	10010	01011	01112000
<i>Erechtia</i> sp.	20022	21000	10010	01010	01112???
<i>Eunusa concolor</i> Fonseca	00000	00000	00000	00010	00110000
<i>Havilandia pruinosa</i> (Haviland)	00001	21100	00110	11000	11100001
<i>H. hypsoproroides</i> gen. & sp. n.	00101	21100	00110	11000	11000001
<i>Kronides</i> sp.	00101	11010	00010	00010	01010020
<i>Enchenopa beebei</i> (Haviland)	21001	21010	00010	00010	01011020
<i>Leioscyta</i> sp. A	10001	21000	00010	00010	00010010
<i>Leioscyta</i> sp. B	20002	21000	10010	00010	01112000
<i>Lewdeitzia lunata</i> ♂ gen. & sp n.	20101	21000	00010	00010	01010000
<i>Lewdeitzia lunata</i> ♀	20101	21000	00010	00011	01010000
" <i>Membracis</i> " <i>ferruginea</i> (Funkh.)	21000	00000	00010	00010	11110000
<i>Membracis foliata</i> (L.)	22000	00000	01010	00010	01011020
<i>Membracis carinulata</i> Richter	21001	11010	01010	00010	01011000
<i>Phyllotropis cingulata</i> (Germar)	22101	11000	01010	00010	01011020
<i>Folicarina bicolor</i> Sakakibara	22101	11010	01010	00010	01010000
<i>Paragara nigra</i> (Funkhouser)	00001	?2000	00010	00010	00110100
<i>Tritropidia</i> sp.	11101	21001	00010	00010	00110100
<i>Tylopelta gibbera</i> (Stål)	20002	21011	00010	00010	01010000
<b>Talipedini</b>					
<i>Trinarea appendiculata</i> (Fonseca)	20112	21000	10010	12011	01112010
<i>Trinarea</i> sp. A	20022	21000	10010	12010	01112???

bracini except *Bolbonotodes*, which is known only from the ♀ holotype, and *Campylenchia*, which is identical to *Enchenopa binotata* for the included characters. Because *Lewdeitzia* is dimorphic for character 18, we included the male and female in the data as separate OTUs. The tribe Talipedini was represented by two species. The other membracine tribes, which are invariant for most of the characters, were each represented by one OTU.

A species belonging to the sister group of Membracinae (Dietrich and Deitz 1993), *Dysyncritus intectus* Fowler (type species of the genus; subfamily Heteronotinae) was chosen as the outgroup. Although clearly a member of Heteronotinae by virtue of the single r-m crossvein in its forewing, *D. intectus* shares certain features with Membracinae that are absent in other Heteronotinae. The metathoracic tibiae have cucullate setae enlarged in rows I and II but reduced

Table 2. List of apomorphies for the cladogram (Fig. 3) based on ACCTRAN character state optimization (Swofford 1990); other equally parsimonious optimizations are possible. Terminal taxa without apomorphies in the data are not listed. Nonhomoplasious changes are indicated by \*.

Node	Apomorphies
52	14 (1), 22 (1)
51	5 (2), 6 (2), 7 (1)
50	11 (1)*, 25 (0 → 2)
49	4 (2), 17 (1)
47	16 (1), 17 (2)
46	3 (1), 4 (0)
45	23 (0)
44	10 (1)
43	5 (1)
42	1 (1), 22 (0)
41	23 (1), 26 (1)
40	3 (1)
39	6 (1), 27 (2)
38	9 (1)
37	2 (1), 25 (1)
36	12 (1)*
35	27 (0)
34	9 (0)
33	2 (2)
32	6 (2)
31	1 (0), 17 (1)
30	8 (1), 13 (1), 16 (1), 19 (0)*, 21 (1), 24 (0), 28 (1)*
Heteronotinae	23 (0), 24 (0)
Aconophorini	5 (0), 6 (0), 7 (0), 18 (1), 25 (1)
<i>Havilandia pruinosa</i>	3 (0), 23 (1)
Hypsoprorini	8 (1), 13 (1), 18 (1)
<i>Enchenopa beebei</i>	3 (0)
<i>Membracis foliata</i>	3 (0), 5 (0), 6 (0), 7 (0)
<i>Membracis carinulata</i>	3 (0)
<i>Folicarina</i>	2 (2), 25 (0)
<i>Kronides</i>	1 (0)
<i>Lewdeitzia</i> ♀	20 (1)
<i>Paragara</i>	1 (0), 7 (2)
<i>Tritropidia</i>	2 (1), 3 (1), 10 (1)
<i>Leioscyta</i> sp. A	27 (1)
<i>Bolbonota</i>	1 (1), 7 (2), 17 (1), 26 (1)
<i>Tylopetla</i>	9 (1)
Hoplophorionini	1 (0), 7 (2), 14 (0), 15 (1)*, 18 (1), 22 (0), 23 (0)
<i>Trinarea appendiculata</i>	4 (1), 20 (1), 27 (1)
<i>Erechtia bicolor</i>	20 (1)
<i>Membracis foliata</i>	2 (1), 21 (1)
<i>Eunusa</i>	1 (0)

in row III, a condition heretofore unknown outside of Membracinae, and forewing vein R is initially divided into R<sub>1</sub> and R<sub>s</sub>.

We analyzed the data (Table 1) using Hennig86 version 1.5 (Farris 1988) and PAUP version 3.0s (Swofford 1990). Exact algorithms (guaranteed of finding minimal length trees) proved too time-consuming, so we used the command sequence "mh; bb\*" of Hennig86 and the heuristic search with Tree-Bisection-Reconnection branch swapping (TBR) and MULTIPARS of PAUP. Among the 10 multistate characters, only characters 2 and 25 were arranged *a priori* in transformation series; thus only these 2 characters were treated as ordered (additive). Initially, we assigned all characters weight = 1. To find trees supported by the most consistent characters, we used the successive weighting facility of Hennig86 (command sequence "xs w; mh; bb\*;" ). We compared the lengths of trees resulting from weighted and unweighted analyses by resetting the weight of each character to 1 (command sequence "ccode /1.; xsteps 1;").

## RESULTS AND DISCUSSION

Hennig86 and PAUP yielded identical results for the unweighted analyses. Both found 4 equally most parsimonious trees of length = 88, consistency index (excluding autapomorphies) = 0.402, and retention index = 0.651. One of four most parsimonious trees is presented in Fig. 3. The others differ in whether the *Erechtia* species form a clade together or with *Trinarea* sp. A, and whether node 49 is supported. None of these 4 trees was preferred by successive weighting, which stabilized after 2 iterations at 71 trees of lengths 90–92, based on all character weights = 1.

Component 47 (Fig. 3) confirms Deitz's (1975) hypothesis that the closest relative of Hoplophorionini is Talipedini, which is a para- or polyphyletic group. Both tribes are apparently derived from Membracini, which is also apparently ancestral to Hypsoprorini and Aconophorini.

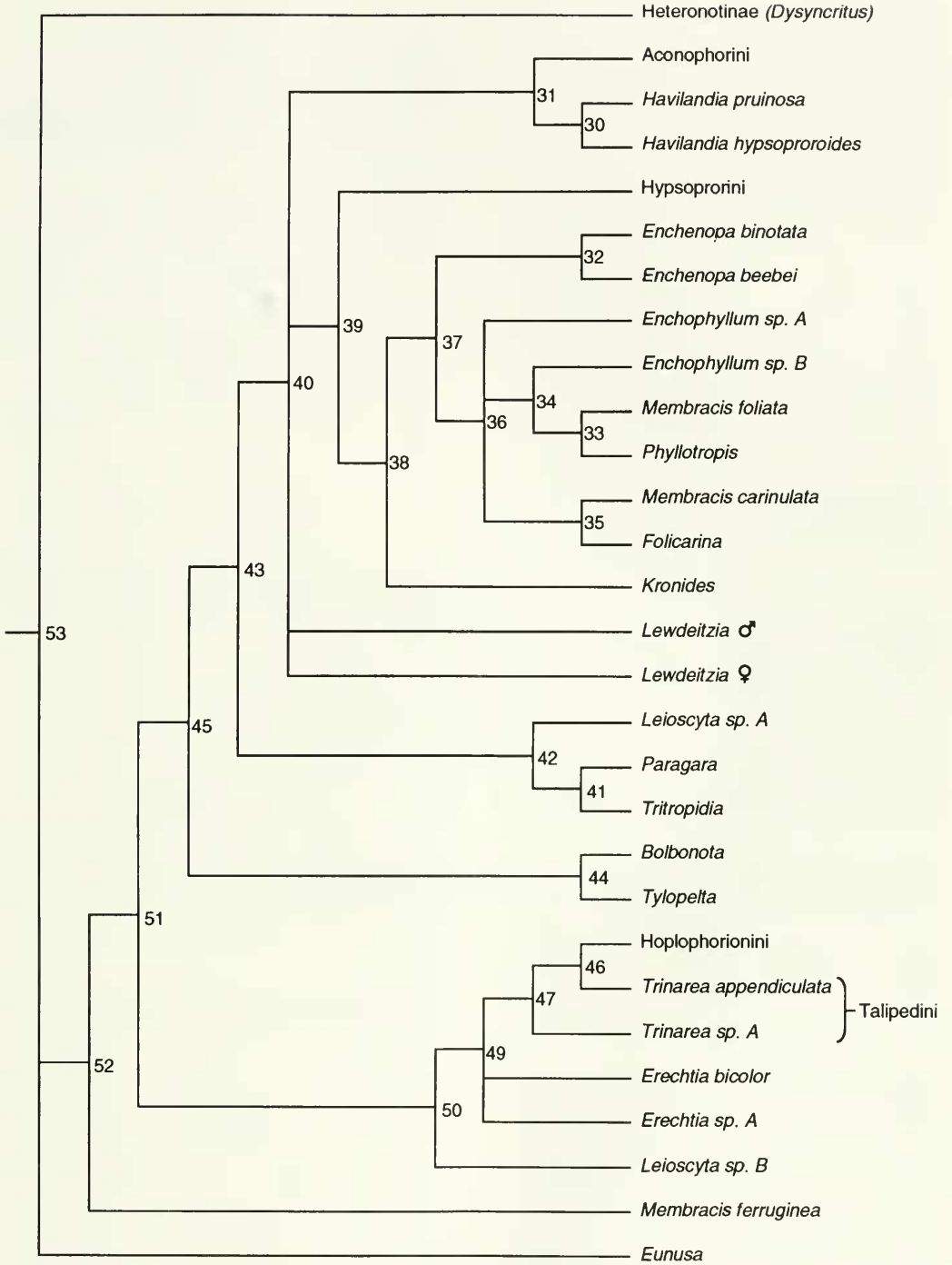


Fig. 3. Hypothesized cladistic relationships among Membracinae. Apomorphies are listed in Table 2.

Aconophorini, Hypsoprorini, and Hoplophorionini are diverse monophyletic groups with distinct morphologies and behaviors, so recognition of additional tribes for genera currently placed in Membracini seems preferable to treating all the tribes of Membracinae as synonyms. However, because some genera of Membracini (*Membracis* and *Leioscyta*) are polyphyletic and others are defined by individual features of the pronotum or forewing (Funkhouser 1951), the creation of new tribes should await species-level analyses that clarify the limits of genera within the two complexes.

One problematic complex of genera includes *Folicarina*, *Phyllotropis*, *Membracis*, and *Enchenophyllum*, which, apart from the plesiomorphic horn in the latter genus, are distinguished from each other only by combinations of four pronotal features: (1) median carina extensively compressed into a plate-like carina or not; (2) metopidium with ventral lobe or not; (3) dorsolateral carinae present or not; and (4) oblique metopidial carinae present or not. *Membracis* exhibits the greatest variation, including among its species both states of all four characters (as examples of [1] and [2], *M. foliata* vs. *M. mexicana* Stål; of [3], *M. flava* Richter vs. *M. mexicana*; of [4], *M. carinulata* vs. *M. humilis* Fowler). The evolutionary polarities of these features need to be determined to establish better generic limits in this complex. The stability of the current genera is especially precarious because none is defined by a single feature—only by combinations.

The other problematic complex includes *Leioscyta* and its relatives (key couplets 14–20, and *Havilandia*). *Leioscyta* includes species with and without dorsolateral carinae and foliaceous mesothoracic tibia, and differs from the other genera only by the absence of their diagnostic (and seemingly apomorphic) traits, rather than by any synapomorphies of its own. Even the outgroup, *Dysyncritus intectus*, would fit the present concept of *Leioscyta* were it not for the fea-

tures distinguishing their respective subfamilies. Thus, *Leioscyta* probably comprises a diverse and polyphyletic set of species retaining different ancestral features, and is in great need of further work. Our preliminary estimate provides a framework for such studies.

Although some problems remain to be solved, other nomenclatural changes are already due. The *Leioscyta*-complex differs from the *Membracis*-complex in having coarser pronotal punctation. This feature was disregarded by Richter (1947) when he described the new species *Membracis micaniae* and by Fonseca and Diringshofen (1969) when they referred *L. ferruginea* Funkhouser to *Membracis*. Both species should be considered Membracini *incertae sedis* until generic limits in the *Leioscyta*-complex are better resolved. The *Leioscyta*-complex differs from *Enchenopa* in lacking oblique metopidial carinae, but not in lacking an anterior horn (e.g. males of *E. permutata* Van Duzee are hornless). We therefore refer *L. beebei*, whose holotype (BMNH) has oblique metopidial carinae but lacks a horn, to *Enchenopa*, creating the new combination *E. beebei* (Haviland).

Our analyses support recognition of the new genera *Havilandia* and *Lewdeitzia*. The most parsimonious trees indicate that *Havilandia* is the sister group of Aconophorini, but the genus shares at least one derived feature with some Hypsoprorini (character 8: pronotal horn with a pair of anteroventral carinae) and trees placing *Havilandia* as the sister group of Hypsoprorini required only one additional step. Although we included no characters in the analysis to unite the male and female of *Lewdeitzia*, the genus clearly represents a lineage distinct from other Membracini and therefore merits formal recognition. Our provisional placement of *Havilandia* and *Lewdeitzia* in Membracini reflects Deitz's (1975) concept of the tribe, which, for nomenclatural stability, is retained at present.

## ACKNOWLEDGMENTS

We are indebted to R. L. Blinn (NCSU), Mick Webb, and Peter Broomfield (BMNH) for lending specimens. L. L. Deitz, R. W. Hodges, P. M. Marsh, H. H. Neunzig, T. K. Wood, and two anonymous reviewers critically reviewed earlier versions of the manuscript. This research was supported, in part, by the North Carolina Agricultural Research Service, North Carolina State University, Raleigh, the University of Connecticut Department of Ecology and Evolutionary Biology, and a National Science Foundation Graduate Fellowship (to SHM).

## LITERATURE CITED

- Deitz, L. L. 1975. Classification of the higher categories of the New World treehoppers (Homoptera: Membracidae). North Carolina Agricultural Experiment Station Technical Bulletin 225: 1-177.
- Deitz, L. L. and C. H. Dietrich. 1993. Superfamily Membracoidea (Homoptera: Auchenorrhyncha): I. Introduction and revised classification with new family-group taxa. *Systematic Entomology* 18: 287-296.
- Dietrich, C. H. 1989. Surface sculpturing of the abdominal integument of Membracidae and other Auchenorrhyncha (Homoptera). *Proceedings of the Entomological Society of Washington* 91: 143-152.
- Dietrich, C. H. and L. L. Deitz. 1991. Revision of the Neotropical treehopper tribe Aconophorini (Homoptera: Membracidae). North Carolina Agricultural Research Service Technical Bulletin 293: 1-134.
- . 1993. Superfamily Membracoidea (Homoptera: Auchenorrhyncha). II. Cladistic analysis and conclusions. *Systematic Entomology* 18: 297-311.
- Farris, J. S. 1988. HENNIG86 reference, version 1.5. Computer program and documentation, published privately, not paginated.
- Fonseca, J. P. da, and R. von Diringshofen. 1969. Contribuição ao conhecimento dos membracideos neotropicos (Homoptera: Membracidae, VI). *Arquivos do Instituto Biológico, São Paulo* 36: 143-161.
- Funkhouser, W. D. 1940. New Peruvian Membracidae (Homoptera). *Journal of the New York Entomological Society* 48: 275-292.
- . 1951. Homoptera fam. Membracidae. *Genera Insectorum* 208: 1-383.
- Goding, F. W. 1926a. New Membracidae, I. *Journal of the New York Entomological Society* 34: 243-246.
- . 1926b. Classification of the Membracidae of America. *Journal of the New York Entomological Society* 34: 295-317.
- . 1929. The Membracidae of South America and the Antilles. IV. Subfamilies Hoplophorioninae, Darninae, Smiliinae, Tragopinae (Homoptera). *Transactions of the Entomological Society of America* 55: 197-330.
- Haviland, M. D. 1925. The Membracidae of Karababo, Bartica District, British Guiana, with descriptions of new species and bionomical notes. *Zoologica [New York]* 6: 229-290.
- Loye, J. E. 1992. Ecological diversity and host plant relationships of treehoppers in a lowland tropical rainforest (Homoptera: Membracidae and Nicomiidae), pp. 280-289. *In* Quintero, D. and A. Aiello, eds., *Insects of Panama and Mesoamerica: Selected Studies*. Oxford University Press, Oxford.
- McKamey, S. H. 1992. Reappraisal of the Neotropical treehopper genus *Eumusa* Fonseca (Homoptera: Membracidae), with ecological notes. *Annals of the Entomological Society of America* 85: 253-257.
- McKamey, S. H. and L. L. Deitz. 1991. Nomenclatural changes in the treehopper tribes Hoplophorionini, Smiliini, and Talipedini (Homoptera: Membracidae). *Proceedings of the Entomological Society of Washington* 93: 193-196.
- Richter, L. 1947. Membracidae Colombianae. *Revisión de las especies Colombianas del género Membracis*. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 7: 382-403.
- Sakakibara, A. M. 1976. *Sphongophorus gracilis* Sakakibara, 1971—*notas complementares*. (Homoptera: Membracidae). *Atas da Sociedade de Biologia do Rio de Janeiro* 18: 1-2.
- . 1992. Sobre alguns Membracini (Homoptera, Membracidae): *Notas taxônomicas e descrições de gênero e espécies novos*. *Revista brasileira Entomologica* 36: 93-100.
- Strümpel, H. 1986. Bemerkungen zur protektiven Mimese von Larven der neotropischen Membracide *Leioscyta spiralis* Haviland, 1925 (Homoptera, Membracidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* 8: 281-284.
- Strümpel, H. and R. Strümpel. 1978. Die Membraciden-Fauna Kolumbiens 4. Die Gattung *Tritropidia* Stål, 1869. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* 6: 133-149.
- Swofford, D. L. 1990. PAUP, Phylogenetic Analysis Using Parsimony, Version 3.0. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

- Wood, T. K. 1984. Life history patterns of tropical membracids (Homoptera: Membracidae). *Sociobiology* 8: 299-344.
- . 1993a. Diversity in the New World Membracidae. *Annual Review of Entomology* 38: 409-435.
- . 1993b. Speciation of the *Enchenopa binotata* complex (Insecta: Homoptera: Membracidae), pp. 299-317. *In* Lees, D. R. and D. Edwards, eds., *Evolutionary Patterns and Processes*. Academic Press, London.
- Wood, T. K. and G. K. Morris. 1974. Studies on the function of the membracid pronotum (Homoptera). I. Occurrence and distribution of articulated hairs. *Canadian Entomologist* 106: 143-158.